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REVIEW ARTICLE

Role of brassinolide in enhancing plant tolerance to salinity stress

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Abstract

Salinity stress is a major constraint to global agriculture, reducing crop yields, degrading arable land and causing economic losses. In many regions, it is intensified by factors such as seawater intrusion, poor irrigation practices and climate-related changes in water availability. While mild salinity may not severely hinder growth, high salinity disrupts ion homeostasis, induces oxidative stress and impairs physiological processes including water and nutrient transport, leading to stunted growth and reduced biomass. Brassinolide (BL), a naturally occurring plant steroid hormone, plays a pivotal role in mitigating salinity stress by regulating ion balance, enhancing antioxidant defense systems, modulating stress-responsive gene expression (e.g., ion transporters, antioxidant enzymes) and promoting growth and development. Its exogenous application through foliar sprays, seed priming or soil treatments has shown promise in improving salt tolerance. This review outlines the mechanisms of salinity stress in plants and highlights the role of BL in alleviating its effects, with emphasis on signalling pathways, ion homeostasis, regulation of Na/H antiporters and reactive oxygen species (ROS) scavenging.

Keywords: antioxidant defense; Brassinolide; ion transporters; plant growth regulation; salinity stress; stress signalling

Introduction

The biggest challenge in agriculture in this era is to feed the fastgrowing population from a gradually reducing fertile land area. Around one billion hectares of total area, which accounts approximately 7 % of the earth is currently facing salinity stress issues (1). While many of these problems are because of natural biogeochemical processes, however about 30 % is due to human induced salinization particularly for of irrigation system (2). The use of lower-quality irrigation water exacerbates soil salinity, while additional sources include seawater intrusion, wind-blown (aeolian) salt deposition and salt release from the weathering of parent materials. Climate change further contributes by increasing saltwater inundation in coastal regions and altering water availability, thereby intensifying irrigation demands. Salinity stress refers to the presence of excessive amounts of soluble salts in the soil or water surrounding plant roots, which can adversely affect plant growth and productivity (3). It influences many physiological processes including water uptake, osmotic balance, nutrient acquisition and photosynthesis. High salt concentrations cause ion toxicity due to increased $Na^+$and Cl^- levels, leading to tissue damage (4). Salinity stress also aggravates oxidative stress, inhibits growth and causes nutrient imbalances. However, certain plants have evolved specific salt tolerance mechanisms to cope with these conditions (5). Brassinolide, a member of the brassinosteroid group–polyhydroxylated steroidal phytohormones–was first identified in the pollen grains of *Brassica napus* in the early 1970s (6, 7). It plays a key role in multiple physiological processes such as growth, development and adaptation to environmental stresses (8, 9). BL is involved in cell expansion and growth by regulating genes related to cell wall synthesis and modification, promoting larger cell size and enhanced tissue growth (10).

BL can increase seed germination by promoting endosperm rupture and reducing the inhibitory effects of Abscisic Acid (ABA) (11). Leaf development is also influenced by BL (12). In terms of reproductive development, BL regulates flower formation, pollen germination and fertilization, thereby supporting successful pollination and contributing to fruit development and seed production (13). BL can delay senescence and aging processes in plants by regulating genes associated with chlorophyll degradation and senescence, thus extending the functional lifespan of leaves (14). It is very important for plant stress responses, helping plants to tolerate drought, salinity, cold, heat and oxidative stress by regulating antioxidant systems, osmotic balance and genes responsible for stress (6). It acts as a molecular signal, transmitting growth and developmental signals within the plant (15). External application of BL has been shown to promote flowering and fruit development in mango (13), strawberry (16), leading to higher fruit set, larger fruits and increased yield in various crops (17). The primary goal of this review paper is to systematically analyze and enumerate the results of recent research, providing a comprehensive understanding of the mechanisms by which BL influences responses to salinity stress. This review critically evaluates the efficacy of BL in enhancing salt tolerance by synthesizing and analysing findings from recent experimental studies, including physiological, biochemical and molecular research on various crop species. The aim is to provide an integrated understanding of BL-mediated mechanisms, highlight current knowledge gaps and identify priority areas for future investigation to guide both applied and fundamental research in salinity stress management.

Mechanisms of salinity stress

Salinity refers to the concentration of dissolved salts in soil or water, commonly measured in parts per thousand (ppt), milligrams per litre (mg L^{-1}) or electrical conductivity (dS m^{-1}) (18). High salinity reduces water uptake, disrupts nutrient balance and can cause sodium and chloride toxicity, ultimately lowering crop yields. As per status report on hydrology, in India, it is prevalent in arid and semi-arid regions such as Rajasthan, Gujarat, Punjab, Haryana and coastal belts (19). Causes include seawater intrusion, saline irrigation water, poor drainage, saline groundwater up flow and unsustainable farming practices. Effective management requires improved irrigation, drainage and salt-tolerant crop cultivation. Salinity stress has harmful effect on plant physiological processes through many mechanisms (20). Firstly, it causes osmotic stress by reducing water availability and hindering cell expansion and development. Secondly, it causes ionic toxicity as excessive salts accumulate in plant tissues, disrupting cellular processes and causing ion imbalances. Plant suffered from salinity stress leads to the evolution of reactive oxygen species (ROS) including superoxide (O), hydroxyl radicals (OH) and hydrogen peroxide (H_2O_2). This occurs through mechanisms such as ion imbalance, oxidative burst mediated by NADPH (nicotinamide adenine dinucleotide phosphate, reduced form) oxidases, disruption of the electron transport chain and enzymatic reactions. The production of ROS can cause cellular damage, affecting lipids, proteins and DNA (21). Salinity stress also disrupts the balance of essential mineral ions, affecting nutrient uptake and transport (22). This stress also causes hormonal imbalance, impairs morphology, triggers genetic and molecular deviations and interferes with normal growth and development processes (23). Salinity stress disrupts ion homeostasis and osmotic balance in plants by causing an imbalance of ions and reducing water availability (24). When plant is exposed to high salt concentrations, it experiences an influx of sodium (Na^+) and chloride (Cl^-) ions into its root system. This disturbs the ion homeostasis, as plants typically maintain a precise balance of important ions such as K^+ (potassium), Ca^{2+}(calcium) and Mg^{2+} (magnesium) within their cells. The excessive accumulation of Na^+ ions disrupts this balance and can interfere with vital cellular processes (25). High salt levels in the surrounding environment create an osmotic imbalance (26). The presence of salts outside the plant cells increases the osmotic potential, reducing the availability of water for plant uptake. As a result, plants unable to maintain adequate water, leading to osmotic moisture stress and cellular dehydration (27).

Brassinolide as a plant hormone

Brassinolide has vital role in influencing various plant physiological processes including growth, development and stress adaptive response (Table 1 & Fig. 1). It is involved in promoting cell elongation, cell division and differentiation, leading to increased plant growth and biomass (28). Brassinolide also influences seed germination, adventitious root development, flowering and fruit development (29-31). One of the key functions of BL is its role in promoting hypocotyl elongation (32). It stimulates the elongation of cells in the stem, resulting in increased plant height (33). Additionally, BL regulates leaf expansion, leading to larger leaf size and increased photosynthetic capacity. This hormone is also involved in the control of vascular tissue development, which ensures efficient transport of water, nutrients and hormones throughout the plant. It prolongs the life of leaves by delaying

Table 1. Function of brassinolide in plant physiological processes

Sl. no.	Role of BL	Mechanism	Crop	Reference
1	Cell expansion and elongation	Modulating gibberellin metabolism	Rice	36
2	Hypocotyl elongation	Expression of auxin responses genes; BZR1/BES1 interacts with auxin response factors (ARFs)	*Arabidopsis*	37
3	Cell division and differentiation	CycD3 induction pathway; BZR1/BES1 directly bind to the promoter region of *CycD3* genes	*Arabidopsis*	38
4	Seed germination	Break seed dormancy, antioxidative defenses	*Brassica juncea*	39
5	Regulating fiber elongation	*GhBES1.4*-mediated regulation of fiber development	Cotton	40
6	Root development	BR signaling via BRI1 KINASE INHIBITOR1	Potato	41
7	Flowering and fruit development	Induced parthenocarpic growth	Cucumber	42
8	Stress responses	Differentially expressed genes (DEGs)	Tomato	43
9	Defense against pathogens	Expression of *Br* genes; hormonal signaling	Barley	44
10	Senescence regulation	Regulating its chlorophyll metabolic pathway and endogenous hormones	*Brassica rapa* subsp. *chinensis*	34
11	Vascular tissue differentiation	Govern stem vascular cell division; expansion; influence cell cycle progression and interact with auxin and other hormones to ensure proper stem growth as well as	*Brassica* spp.	28

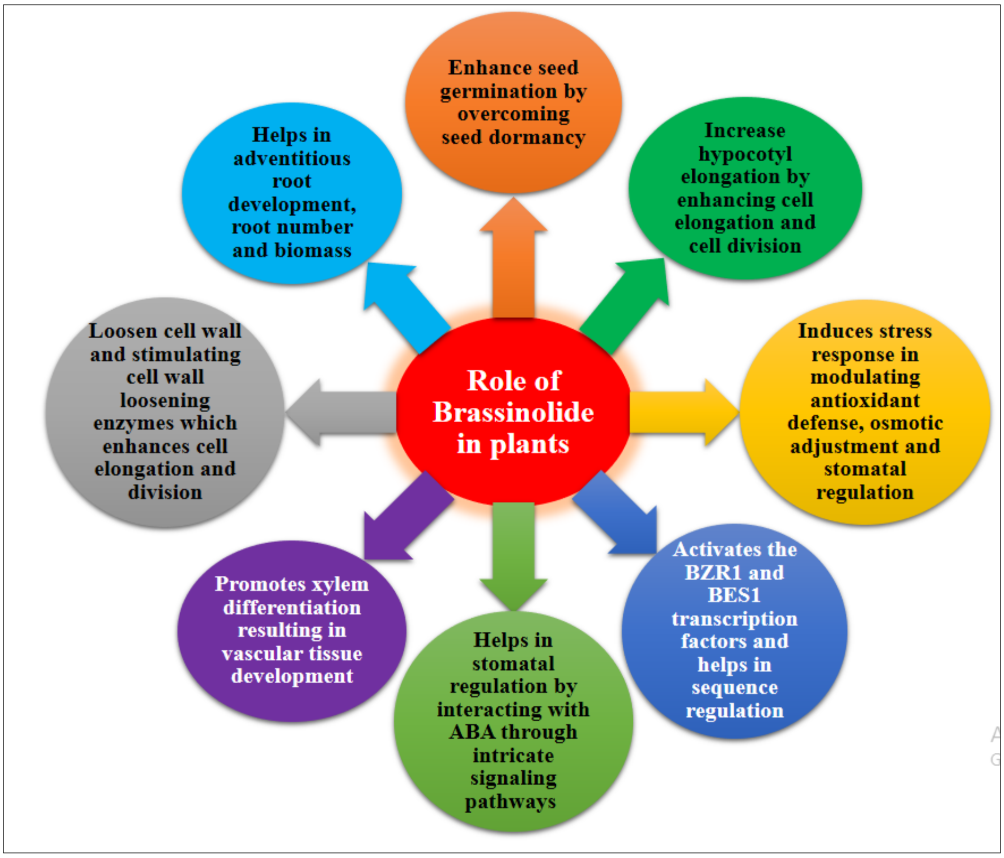

Fig. 1. Function of brassinolide in plant physiological processes.

senescence. It contributes to sustained photosynthetic activity by controlling the expression of genes linked to ageing (34). Brassinolide is known to enhance plant tolerance to various abiotic stresses such as high and low temperatures, drought, salinity and heavy metals. Brassinolide influences stomatal aperture, affecting gas exchange and water loss (35). It helps plants adapt to adverse conditions by influencing the expression of stress-responsive genes and promoting the synthesis of protective compounds. Furthermore, BL has been found to improve plant resistance against pathogens by activating defense mechanisms.

Signaling pathways and mechanisms of brasssinolide action

Brasssinolide signalling pathway is complex and tightly regulated, it governs various physiological functions such as cell expansion, cell division, root development, flowering, stress responses and defense against pathogens. Fig. 2 represents a simplified version of this signaling pathway. At the core of BL signaling are the cell surface receptors BRI1 and BAK1, which

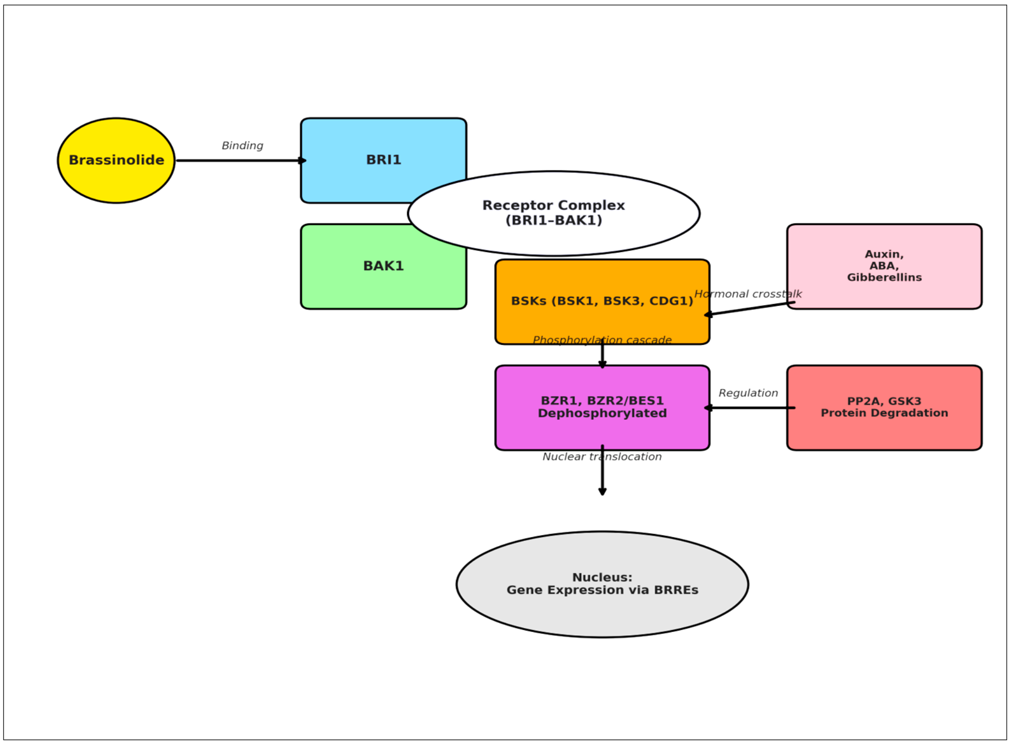

Fig. 2. Signaling pathways and mechanisms of Brassinolide action.

perceive and bind BL. The binding of BL to BRI1 triggers conformational changes and the formation of a receptor complex with BAK1 (15). This receptor complex activates intracellular signalling cascades, known as the brassinosteroid signalling kinases (BSKs) pathway, through a phosphorylation cascade involving multiple protein kinases. Key components of this pathway include BSK1, BSK3 and CDG1 (45). The initiation of this pathway leads to the dephosphorylation and translocation of transcription factors namely BZR1 and BZR2/ BES1 into the nucleus. Once in the nucleus, BZR1 and BZR2/ BES1 control the expression of specific genes by binding to target DNA sequences called brassinosteroid response elements (BRREs) in the promoters of these genes (46). Depending on the context, they can either activate or repress the expression of target genes. These target genes are involved in important processes such as cell elongation, cell division, hormone biosynthesis, stress responses and other physiological processes. Additionally, various hormone-signalling pathways interact with BL signalling including auxin, ABA and gibberellins, allowing for crosstalk and integration of various hormonal signals in plant physiology (47). Furthermore, protein degradation plays an important role in the regulation of BL responses. Proteins like protein phosphatase 2A (PP2A) and glycogen synthase kinase-3 (GSK3) are involved in the degradation of BZR1 and BZR2/BES1, ensuring proper control of BL signalling.

Impacts of exogenous BL on salinity stress

Exogenous BL application alleviates the detrimental effects of salinity stress (Table 2 & Fig. 3), leading to improved plant adaptation, survival and crop productivity under saline conditions (48). BL improves salt tolerance by promoting ion homeostasis, reducing the accumulation of toxic ions and enhancing the activity of ion transporters (49). BL also enhances water relations by increasing water uptake efficiency and reducing water loss through stomatal regulation (50). It boosts antioxidant defense by improving antioxidant enzyme activity and defending plants from oxidative injury. Exogenous application of BL modulates gene expression particularly by upregulating stress-responsive genes associated with salinity tolerance. Such application improves photosynthetic efficiency, promotes growth and development by stimulating root and shoot growth and balances stress-responsive hormones.

Alleviation of ion imbalance: Salinity stress increases the accumulation of Na^+ ions in plant tissues, which can disrupt ion homeostasis and impair plant growth (62). Exogenous application of Brassinolide (BL) can alleviate the negative effects of salinity stress on plants by mitigating ion imbalance (51). BL regulates ion uptake, restricts sodium uptake, enhances the potassium-sodium ratio, stimulates ion transporters and modulates ion channel activity (63). It promotes the uptake of essential minerals while limiting excessive sodium accumulation. BL also enhances the expression of ion transporters, such as SOS1 (sodium/hydrogen antiporter) and stimulates potassium uptake, improving the potassium/sodium ratio (64). Furthermore, BL regulates ion channels such as inward-rectifying K^+ channels to maintain ion balance (65). Overall, BL helps in maintaining ion homeostasis, minimizing the negative consequences of salinity stress on plant physiology. Exogenous BL applications witnessed to enhance the absorption of essential mineral nutrients including potassium, calcium and magnesium, which helps to maintain a favourable balance between Na^+ and other cations, reducing the negative impact of excessive Na^+ accumulation (66). BL treatment has been shown to increase the uptake of potassium and enhance its transport to shoots by activation of K^+ transporters and channels, enhanced proton pump activity (H^+-ATPase) (81) and improved root system architecture (82). As a result, the potassium/sodium ratio is improved, which causes osmotic balance, reducing the negative effects of salinity stress.

Na^+ exclusion and K^+ retention: High salt levels in soil results uptake of excessive Na^+ by plant roots, which can be detrimental to plant growth. BL treatment is shown to enhance

Table 2. Role of Brassinolide in salt tolerance mechanism of different crop species

Sl. no.	Exogenous application (concentration)	Mechanism	Crop	Reference
1	24-epibrassinolide and kinetin (100 nM)	Modulation of antioxidant and osmolyte metabolism	*Solanum lycopersicum*	51
2	24-epiBL (10^{-7} mM)	Maintaining ionic balance (K^+/Na^+); antioxidative enzyme activities	*Glycine max* L.	52
3	24-epibrassinolide (10^{-6} M)	Signaling of nitric oxide and pathways of antioxidant defense	*Brassica juncea* L. cv. varuna	53
4	24-epibrassinolide (2 µM)	Promotion of Ca^{2+} accumulation in roots	*Arabidopsis*	49
5	Brassinosteroids	Regulates over expression of key receptor SlBRI1	*S. lycopersicum*	54
6	24-epibrassinolide (200 mL L^{-1})	Increased leaf gas exchange and water use efficiency	*Ficus carica*	50
7	28-homobrassinolide	Increasing carboxylation efficiency and the activity of ROS scavenging system	*Vigna radiata*	55
8	24-epibrassinolide (1.0 µmol L^{-1})	Activation of antioxidant defense systems	*Oryza sativa* L.	48
9	24-epibrassinolide (0.01 µM)	Activation of antioxidant defense systems	*Zea mays*	56
10	24-epibrassinolide (100 ppm)	Increased osmolytes activities, antioxidants defence system and limiting Na^+ uptake while keeping the K^+ level in leaves stable	*Hordeum vulgare* L.	57
11	24-epibrassinolide seed priming	Prevented the salinity mediated photosynthetic inhibition	*G. max* L.	58
12	Brassinosteroids (0.2 mg L^{-1})	NHX-Type Na^+ (K^+)/H^+ antiporter transcription regulation	*Malus hupehensis*	59
13	24-epibrassinolide (0.1 µM)	Increasing the expression of *AhNHX7* and *AhNHX8* and removing ROS	*Arachis hypogaea*	60
14	24-epibrassinolide, bikinin and brassinazole (0.01 µM – 0.01 µM)	Increased osmolytes activities, antioxidants defence system	*H. vulgare* L.	61

Fig. 3. Impact of BL in plant growth and development under salinity stress.

the exclusion of Na^+ ions from plant roots (47). It helps in regulating the activity of ion transporters, such as the sodium/ hydrogen antiporter (SOS1), which actively pumps Na^+ out of the roots and reduces their accumulation in the shoot tissues (Fig. 3). This sodium exclusion mechanism helps prevent sodium toxicity and maintains a more favourable sodium-to-potassium ratio in plant tissues. Salinity stress often disrupts K^+ homeostasis in plants, leading to potassium deficiency (67). However, exogenous BL application can help retain higher levels of potassium in plant tissues under saline conditions (48). BL enhances the activity of K^+ transporters, such as high-affinity potassium transporters (HKTs), which facilitate the absorption and transport of K^+ ions in roots. BL treatment has been reported to influence the expression of genes involved in potassium uptake and translocation, contributing to improved potassium retention in plants.

Regulation of ion channels and transporters: BL is witnessed to regulate the ion transporter expression and activity such as plasma membrane H^+-ATPases and Na^+/H^+ antiporters (59). These transporters are responsible for maintaining ion gradients across the cell membrane. BL enhances the activity of plasma membrane H^+-ATPases, which helps maintain a favourable electrochemical gradient for nutrient uptake and regulates Na^+ exclusion from the cytoplasm. Exogenous BL application influences the activity of ion channels involved in ion transport. It has been reported to regulate the activity of K^+ channels, including inward-rectifying K^+ channels (KIR) and outward-rectifying K^+ channels (KOR) (68). This regulation helps maintain proper potassium ion uptake, transport and distribution, which is important for osmotic adjustment and stress tolerance in plants.

Reactive Oxygen Species scavenging and antioxidant defense

Exogenous application of BL revealed to alleviate the negative effects of salinity stress on plants by influencing in scavenging of ROS and defense systems of antioxidant (69). Salinity stress often leads to the accumulation of ROS, including H_2O_2, (O_2-) and OH, which can cause oxidative damage to plant cells. BL treatment helps in the scavenging of ROS by improving the activities of antioxidant and non-enzymatic antioxidants. BL treatment enhances the activities of various antioxidant enzymes including peroxidase (POD), superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX) (70). These enzymes play a crucial role in converting SOD to O2- and finally into H_2O_2. CAT metabolizes H_2O_2 into water and oxygen, while PODs detoxify H_2O_2 and organic hydroperoxides. Non-enzymatic antioxidant accumulation includes ascorbic acid (vitamin C), glutathione (GSH) and carotenoids (71). These compounds help reduce ROS directly and protect cellular components from oxidative injury.

Modulation of stress-responsive gene expression

Exogenous BL application has been shown to regulate the action of stress-responsive genes in plants under salinity stress (71). Salinity stress triggers a complex network of gene expression changes to help plants acclimatize and tolerate with the adverse conditions. BL treatment has been found to control the gene expression involved in stress response mechanisms. BL treatment can regulate the expression of genes involved in ion transport and ion channel activities, such as those encoding ion transporters (e.g., SOS1, NHX) and potassium channels (72). BL can influence the associated genic expression with ABA biosynthesis and signaling, as well as those involved in the crosstalk between ABA and brassinosteroids (73). These interactions help regulate stomatal closure, osmotic adjustment and other adaptive responses to salinity stress. BL treatment can activate defense-related genes involved in stress signaling pathways. These genes may include receptor-like kinases (RLKs), pathogenesis related (PR) proteins, heat shock proteins (HSPs) and other stress-responsive genes (74).

Activation of stress-responsive transcription factors and signaling pathways

BL treatment can activate stress-responsive transcription factors, such as BZR/BES transcription factor SlBZR1 favorable regulates BR signalling and salt stress tolerance in tomato and *Arabidopsis* (75). These transcription factors cause the upregulation of stress-related genes by binding to particular DNA sequences in their promoter regions. The upregulated genes are involved in various stress responses including osmotic regulation, detoxification and antioxidant defence. Signalling pathways play a crucial role in the plant's ability to perceive and respond to the stress, leading to adaptive physiological and biochemical changes. One important mechanism involved in plant stress responses is the mitogen-activated protein kinase (MAPK) signalling system. The activation of MAPKs triggers a series of phosphorylation events that regulate the expression of stress-responsive genes, resulting in enhanced stress tolerance (76). Ca^{2+} has key role as messengers in stress signalling. This calcium influx activates calcium-dependent protein kinases (CDPKs) and other Ca-binding proteins, which initiate downstream signalling events. The calcium-mediated signalling pathway is involved in regulating various stress-responsive genes and physiological processes including osmotic regulation, ion transport and antioxidant defence. It can modulate the crosstalk between these hormones to regulate stress responses.

Regulation of NHX-type $Na^+(K^+)/H^+$ antiporter transcription

Exogenous application of BL has been found to alleviate saline stress in plants by influencing the transcription of NHX-type Na^+ $(K^{+})/H^+$ antiporter genes (59). BL activates the brassinosteroid signaling pathway, leading to the activation of transcription factors such as BZR1. These transcription factors bind to specific promoter regions of NHX-type $Na^+(K^+)/H^+$ antiporter genes, resulting in their transcriptional activation. The synthesized NHX proteins function as ion transporters, facilitating the efflux of Na^+ ions from the cytoplasm and its sequestration into vacuoles (77). This mechanism helps maintain ion homeostasis and prevents the toxic effects of sodium accumulation in plant cells under salt stress conditions. NHX proteins function as ion transporters that mediate the exchange of Na^+ and K^+ ions with protons (H^+) across membranes, thus reducing the toxic effects of sodium accumulation in plant cells under salt stress conditions (78).

Efficient ion transport and ion homeostasis

Exogenous application of BL (BL) has been shown to alleviate salt stress in plants by preventing excessive Na^+ accumulation (49). BL treatment influences the activity and expression of ion transporters involved in Na^+ uptake, compartmentalization and efflux (79). It enhances the expression of H^+-ATPases, which facilitate the efflux of Na^+ from cells, preventing its accumulation. Additionally, BL increases the expression of K^+ transporters, promoting the uptake of K^+ ions. This shift in ion transport helps maintain a favourable K^+/Na^+ ratio and reduces Na^+ accumulation in cells. BL treatment affects the activity of ion channels involved in Na^+ transport. It has been found to inhibit the activity of non-selective cation channels (NSCCs), which are responsible for Na^+ influx into cells (80). By reducing Na^+ influx, BL helps prevent excessive Na^+ accumulation under salt stress conditions.

Regulation of Salt Overly Sensitive (SOS) pathway

The SOS pathway is a key signalling pathway involved in salt stress responses. BL treatment enhances the expression and activity of SOS pathway components including SOS1 and SOS3/SOS2 (59). This activation of the SOS pathway facilitates Na^+ efflux from cells, reducing its accumulation in the cytoplasm. The SOS pathway consists of several components, including SOS1 (a plasma membrane Na^+/H^+ antiporter), SOS2 (a serine/threonine protein kinase) and SOS3 (a calcium sensor). Interaction between BL and SOS components leads to the activation of SOS2 kinase activity, which subsequently phosphorylates and activates the SOS1 antiporter. By regulating the SOS pathway, BL helps plants maintain ion homeostasis and minimize the negative effects of salt stress (79).

Conclusion

Exogenous application of BL offers significant potential for enhancing plant stress tolerance, stimulating growth and improving productivity and resilience under salt-affected conditions. Study reported that BL induce tolerance to salinity stress at specific concentration depending upon the crop species (83). When plants suffered salinity stress, BL helps regulate ion homeostasis by increasing the uptake of essential nutrients like potassium while reducing the uptake of toxic ions such as Na^+ and Cl^-. It also improves osmotic stress tolerance of plants by increasing the accumulation of compatible solutes, preventing water loss and maintaining cellular water potential. Additionally, BL enhances the antioxidant enzymes activities and increases the content of non-enzymatic antioxidants, protecting plants from oxidative damage caused by ROS. The implications of BL application include improved salt tolerance, enhanced productivity, sustainable agriculture in saline environments and the induction of stress priming effects, leading to improved stress tolerance in subsequent salinity stress episodes. Future research should focus on (i) elucidating the molecular mechanisms and signaling pathways underlying BL-mediated stress tolerance, (ii) exploring genotype-specific responses to optimize its use in breeding programs, (iii) developing efficient, cost-effective and scalable application methods for field conditions and (iv) integrating BL treatment with other agronomic and biotechnological approaches to promote climate-resilient and sustainable crop production in salt-affected ecosystems.

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Authors' contributions

JP, PD, KKJ did the conceptualization of article. Collection of research data and interpretation was done by JP, TM and KP[1]. AJ, GK, KP[2] and CVR prepared the manuscript. Language editing was done by HP and DP. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

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